

### Summary

#### *The patterns of the palate-ridges of African Sciuridae*

The paper deals with the pattern of palate-ridges in African Sciuridae. Though agreeing in the basic pattern, special differences exist between genera and species, which concern mainly the number of intermolar ridges. The hypothetical, but suggesting conclusion is pointed out, that the increase of the ridges is due to the secondary development of "interridges". Considered in connection with other morphological criteria, the pattern of the palateridges can be of taxonomic value, as it is shown in some examples.

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## Chromosomes of some species of *Gerbillus* (Mammalia Rodentia)

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Forty to fifty species of rodents comprise the genus *Gerbillus* and occur within that part of the Great Palaeartic Desert from the Sahara and Sahel of North Africa to the Indian Desert. Current classifications of *Gerbillus* are based upon the pioneering studies of LATASSE (1880—82), which recognized four subgenera including *Gerbillus*, *Dipodillus*, *Hendecapleura* and *Tatera*, of which the last is presently regarded as generically distinct (ELLERMAN 1940). Among recent workers ELLERMAN (1940) acknowledged that the remaining three of LATASSE's subgenera are related and treated them taxonomically as a single genus, *Gerbillus*, containing two subgenera, *Gerbillus* and *Dipodillus* (including *Hendecapleura*). In contrast PETTER (1959) divided the same froms into two genera, *Gerbillus* and *Dipodillus*, the latter including the subgenera *Dipodillus* and *Hendecapleura*. A distinct need exists for a modern taxonomic revision of these rodents, especially at the species level. Until such a review is available we will refer to all species as *Gerbillus* without reference to sub-generic divisions.

This study presents a summary of the cytogenetic data (including new information and work in progress) for the 20 species of *Gerbillus* analyzed to date and considers the utility of these data for defining taxonomic categories at and above the species level.

## Materials and methods

Thirty-five specimens were studied cytologically and are preserved as vouchers in collections of the University of Michigan Museum of Zoology: *Gerbillus allenbyi* Thomas, 1918, Israel: Ramat Aviv, 2 males; *Gerbillus andersoni* deWinton, 1902, Egypt: km 164 on Cairo-Alexandria Road, 2 males, 1 female; *Gerbillus gerbillus* Olivier, 1801, Egypt: Abu Rawash, 1 male and 2 females; Sinai: El Kaa plain, 1 female; Morocco: 10 km W Zagora 1 female; *Gerbillus perpallidus* Setzer, 1959, Egypt: El Beida, Wadi el Natroun, 1 male; *Gerbillus pyramidum* Geoffroy, 1825, Egypt: Abu Rawash, 2 males and 3 females; *Gerbillus* sp. (? = *tarabulli*), Morocco: 10 km W Zagora, 1 male; *Gerbillus campestris* Levaillant, 1857, Morocco: 5 km NE Essouira, 1 male; 20—29 km SW Goulimine, 3 males and 7 females; 5 km S Taroudannt, 2 females; *Gerbillus nanus* Blanford, 1875, Morocco: 29 km SW Goulimine, 1 male and 1 female; *Gerbillus henleyi* deWinton, 1903, Morocco: 29 km SW Goulimine, 1 male and 1 female.

Specimens used in this study were identified using pelage and cranial characters (PETTER 1961; LAY, unpublished data) and by comparison with examples in the collections of the British Museum (Natural History), London, Field Museum of Natural History, Chicago and University of Michigan Museum of Zoology, Ann Arbor. Chromosome preparations from femoral bone marrow and karyotype descriptions follow our earlier techniques (NADLER and LAY 1967). Fundamental number (FN) is computed by counting the total number of autosome and sex chromosome arms to facilitate comparison with previously published material.

## Results

### Hairy-footed *Gerbillus* species

*Gerbillus allenbyi* from Israel have a diploid number ( $2N$ ) = 40 and fundamental number (FN) = 80. The karyotype contains 14 metacentric and 24 submetacentric autosomes, a large submetacentric X and medium-sized submetacentric Y chromosome (Fig. 1).

*Gerbillus andersoni* from Egypt show a  $2N$  = 40 and FN = 80. The morphology of the autosomes and sex chromosomes is virtually identical to that of *G. allenbyi* (Fig. 1).

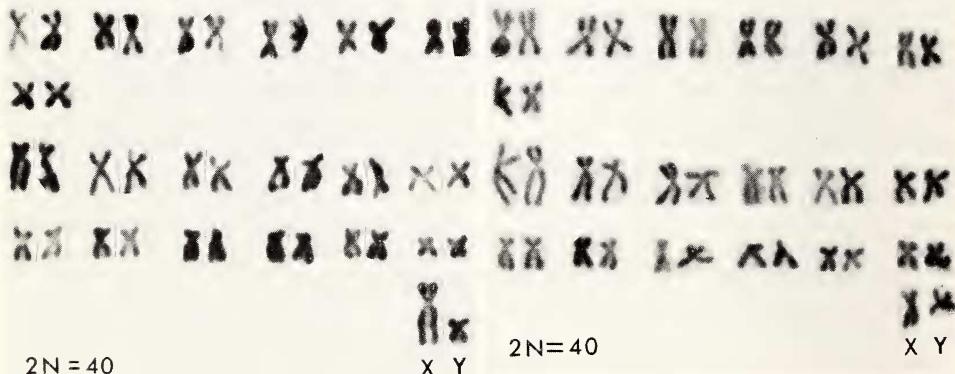


Fig. 1. Karyotypes of male *Gerbillus allenbyi* (left) and male *G. andersoni* (right)

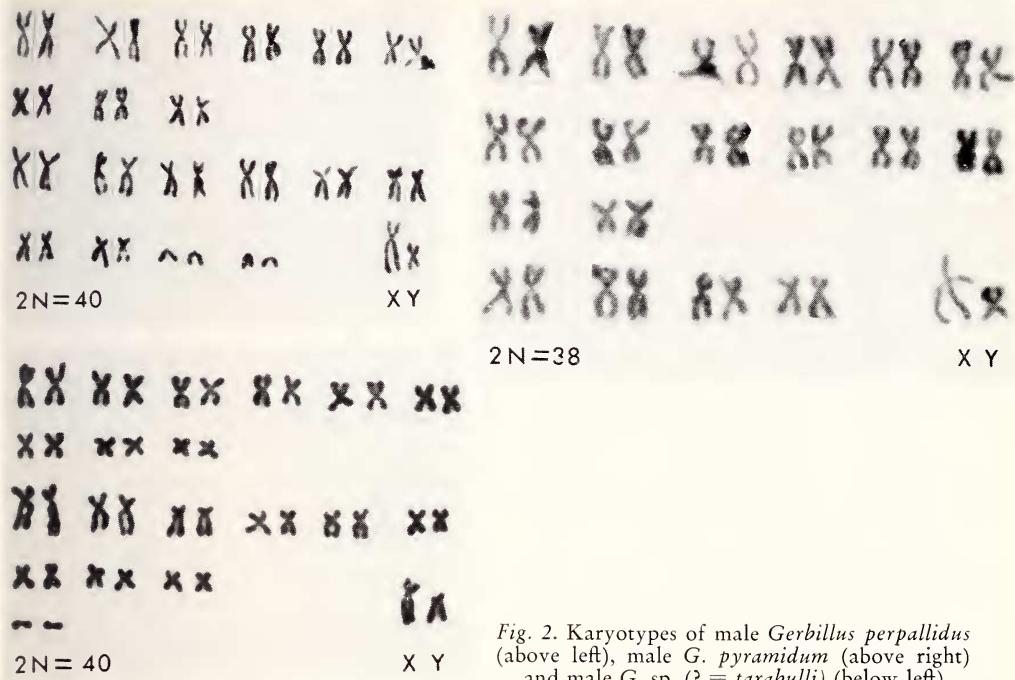


Fig. 2. Karyotypes of male *Gerbillus perpallidus* (above left), male *G. pyramidum* (above right) and male *G. sp.* (? = *tarabulli*) (below left)

*Gerbillus perpallidus* from Egypt exhibit a  $2N = 40$  and  $FN = 76$ . The karyotype contains 18 metacentric, 16 submetacentric and 4 acrocentric autosomes. A large submetacentric, the presumed X, and a small metacentric, presumably the Y constitute the sex chromosomes (Fig. 2).

*Gerbillus pyramidum* from Egypt. reveals a  $2N = 38$  and  $FN = 76$ . There are 26 metacentric and 8 submetacentric autosomes. The X chromosome is a large submetacentric and the Y is a small metacentric (Fig. 2).

*Gerbillus gerbillus* from Sinai and Egypt and Morocco have a  $2N = 42 \text{♀}$ ,  $43 \text{♂}$ , and  $FN = 76 \text{♀}$ ,  $78 \text{♂}$ . The karyotype contains 13 metacentric, 17 submetacentric and 8 acrocentric autosomes. The X is the largest submetacentric in the complement and the two Y chromosomes are medium metacentric and small submetacentric elements (Fig. 3).

*Gerbillus* sp. (? = *tarabulli*) from Morocco possesses a  $2N = 40$  and  $FN = 76$ . The karyotype has 18 metacentric, 18 submetacentric and 2 acrocentric autosomes. Both the X and Y are submetacentric elements (Fig. 2).

#### Naked-footed *Gerbillus* species

*Gerbillus campestris* from Morocco display chromosomal polymorphism with  $2N = 56$ , 57, 58 and  $FN = 68$ . The karyotypes contain 10, 11 or 12 metacentric and submetacentric chromosomes and 48, 46 or 44 acro-

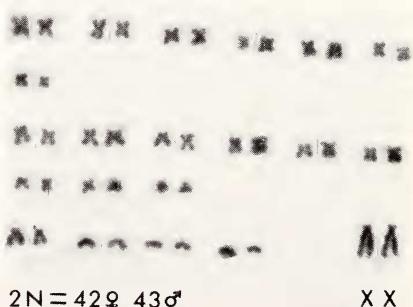


Fig. 3. Karyotype of female *Gerbillus gerbillus* from Egypt: Abu Rawash

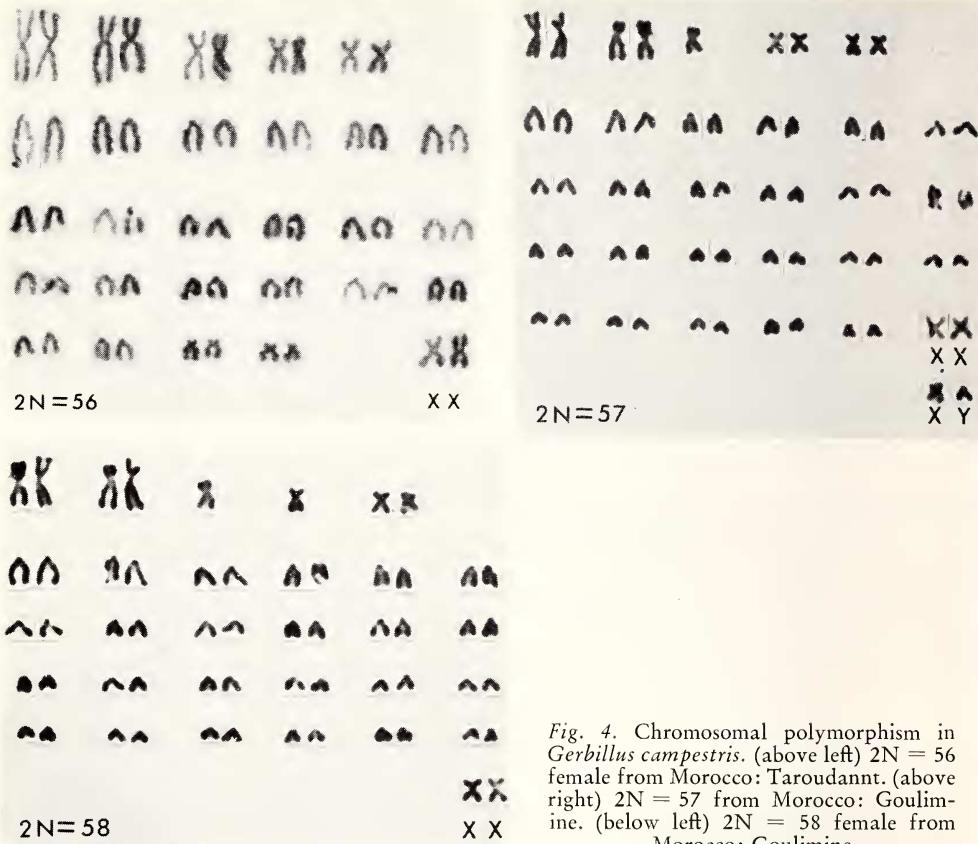


Fig. 4. Chromosomal polymorphism in *Gerbillus campestris*. (above left)  $2N = 56$  female from Morocco: Taroudannt. (above right)  $2N = 57$  from Morocco: Goulimine. (below left)  $2N = 58$  female from Morocco: Goulimine

centric chromosomes, respectively. The X is a medium metacentric and the Y is a small acrocentric element (Fig. 4).

*Gerbillus nanus* from Morocco reveals a  $2N = 52$  and  $FN = 61 \delta, 62 \varphi$ . The karyotype consists of 8 submetacentric and 42 acrocentric autosomes. The X is a large metacentric and the Y is a small acro or subtelocentric chromosome (Fig. 5).

*Gerbillus henleyi* from Morocco possesses a  $2N = 52$  and  $FN = 61 \delta, 62 \varphi$ . The karyotype has 8 submetacentric and 42 acrocentric autosomes. The X is a large submetacentric and the Y is a small acrocentric chromosome (Fig. 5).

### Discussion

Comparison of the chromosomal characteristics summarized in Tables 1 and 2 reveals a number of differences between our data and that reported earlier by MATTHEY (1952, 1953, 1954a, b, 1955), WAHRMAN and ZAHAVI (1955), ZAHAVI and WAHRMAN (1957), and WASSIF et al. (1969). There is no disagreement in the diploid number reported for any species and only slight differences in features of chromosome morphology between our results and those of previous studies. However, as noted in Tables 1 and 2, karyotypes of a number of species have not been published and it is

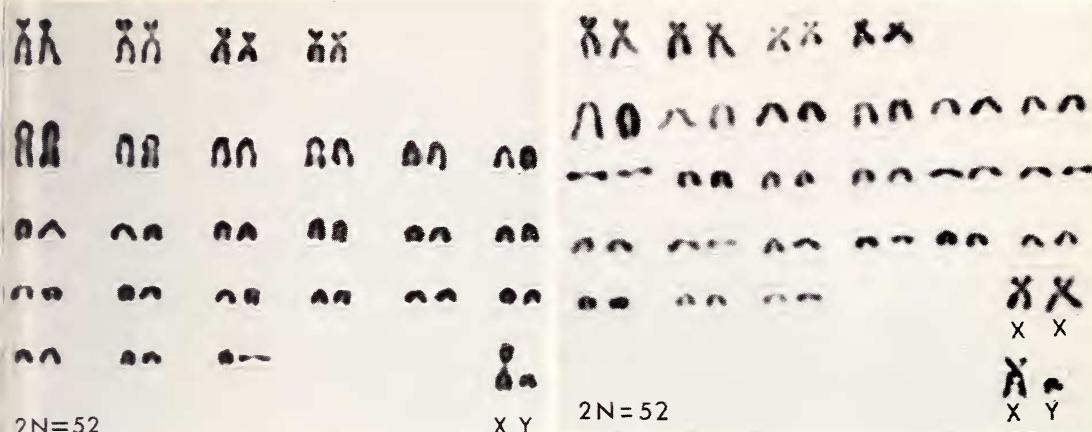


Fig. 5. Karyotypes of male *Gerbillus nanus* from Morocco: Goulimine (left) and *G. henleyi* from Morocco: Goulimine (right)

impossible to confirm whether the differences between our work and that of previous workers are real.

The diploid numbers of the 13 species of hairy-footed *Gerbillus* (= subgenus *Gerbillus*) studied to date range from 38 to 72 and the fundamental number spans 72–80. The diploid numbers of seven species of naked-footed *Gerbillus* (= subgenera *Hendecapleura* and *Dipodillus*) are 52 to 60 and the fundamental numbers are 62 to 68 (Table 1 and 2). The majority of the hairy-footed species possess 20 or more biarmed chromosomes while all of the naked-footed species seemingly show 10 or less, and numbers of acrocentric elements is the reciprocal of that for the metacentrics. These two "categories" of *Gerbillus* are distinct, so far as presently studied, only in fundamental numbers. Diploid numbers and chromosome morphology presently do not lend strong support to the concept of two or more subgenera in the genus *Gerbillus*, although G-band analyses might reveal unrecognized affinities.

It is noteworthy that two species display karyotypic uniformity over a wide range. *G. gerbillus* karyotypes are seemingly identical morphologically from Sinai, Egypt, Algeria and Morocco, a distance of over 4000 kilometers. Specimens of *G. nanus* from Pakistan, Iran, Israel and Morocco appear to have identical karyotypes across a range of more than 8000 kilometers, but material from Israel should be re-examined. Further, *G. aquilus* shows karyotype uniformity across more than 850 kilometers of range in Iran and Pakistan (LAY and NADLER, MS).

Chromosomal polymorphism has been attributed to Israeli and Algerian populations of *G. pyramidum* (WAHRMAN and ZAHAVI 1957; ZAHAVI and WAHRMAN 1957; WAHRMAN and GOUREVITZ 1972). The type locality of *G. pyramidum* is Giza Province, Egypt (cf. ELLERMAN and MORRISON-SCOTT 1951). We have studied topotypical specimens of *G. pyramidum* from Abu Rawash, Giza Province, Egypt and WASSIF et al. (1969) have reported on similar examples from Abu Rawash and El Faiyum to the south. These specimens have a  $2N = 38$ , FN = 76 and all chromosomes are biarmed (Table 1, Fig. 2). The absence of polymorphism in this Egyptian material, the high and variable  $2N$  of 50–66 of the Israeli population and the absence of any known zone of intergradation between these populations suggests that they should be considered as specifically distinct until genetic introgression is demonstrated. MATTHEY (1953) reported  $2N = 40$ , FN = 78 for *G. pyramidum* from Beni Abbes, Algeria and we

Table I

Species	Locality	2N	Autosomes		Sex Chromosomes		FN	Reference
			M + SM	ST + A	X	Y		
<i>G. pyramidum</i>	Egypt: Abu Rawash Egypt: Abu Rawash and Fayyum	38 38	36 36		ISM SM	sM M	76 76	Present paper WASSIF et. al. 1969
<i>G. aquilus</i>	Pakistan: Nushki; Iran: Kerman	38	36		ISM	sSM	76	LAY and NADLER, MS.
<i>G. densesmani</i>	Iran: 16 km SW Shush	38	34	2	IM	sSM	74	LAY and NADLER, MS.
<i>G. allenbyi</i>	Israel: Tel Aviv Israel: Tel Aviv <sup>3</sup>	40 40	38 38		ISM ?	sSM ?	80 80	Present paper WAHRMAN and ZAHAVI 1955
<i>G. andersoni</i>	Egypt: km 164 Cairo-Alexandria Rd. Egypt: Mariyut and Khatatba	40	38		mSM	sM	80	Present paper
<i>G. sp.</i>	Morocco: Aoreira	40	38		?	?	80	WASSIF et. al. 1969
<i>G. sp. (= ? tarabulli)</i>	Morocco: 10 km W Zagora Algeria <sup>3</sup>	40 40	36 36	2 2	ISM SM	mM mM	80 78	LAY, in press Present paper MATTHEY, 1952, 1953; WAHRMAN and ZAHAVI 1955
<i>G. perpallidus</i>	Egypt: Wadi el Natroun	40	34	4	ISM	sM	76	Present paper
<i>G. gerbillus</i>	Egypt: Abu Rawash; Sinai Morocco: 10 km W Zagora Egypt: Abu Rawash Algeria <sup>3</sup> Algeria	♀ 42, 43 32 36—38 34 ?	♂ 42, 43 32 36 34 42, 43	32 32 8 6	ISM ISM Y <sub>1</sub> Y <sub>2</sub> Y <sub>1</sub> Y <sub>2</sub> Y <sub>1</sub> Y <sub>2</sub> ?	Y <sub>1</sub> Y <sub>2</sub> ?	76, 78 76, 79, 81 81—83 ?	Present paper WASSIF et. al. 1969 WAHRMAN and ZAHAVI 1955 MATTHEY 1953, 1954;
<i>G. glaucomys</i>	Pakistan: Rahim Yar Khan Israel: Tel Aviv S to Gaza <sup>3</sup>	♂ 50, 51 20 variable	♂ 50, 51 20 variable	28 variable	ISM ?	<sup>2</sup> Y <sub>1</sub> Y <sub>2</sub> ?	72, 73 ?	LAY and NADLER, MS. WAHRMAN and GOUREVITZ 1972
<i>G. hesperinus</i>	Morocco: Essaouira	58	22	34	ISM	IM	76	LAY, in press
<i>G. sp.</i>	Morocco: Taroudannt	72	6	64	ISM	IM	80	LAY, in press

M = metacentric, SM = submetacentric, St = subtelocentric, A = acrocentric, 1 = large, m = medium, s = small.  
<sup>1</sup>Y<sub>1</sub> = sM, Y<sub>2</sub> = sSM, Y<sub>1</sub> = mM, Y<sub>2</sub> = lA; <sup>3</sup> No karyotype published.

Table 2

Species	Locality	2 N		Autosomes		Sex Chromosomes		FN	Reference
		M	+	SM	ST + A	X	Y		
<i>G. nanus</i>	Morocco: Goulimine; Iran: SW Shush, Kerman; Pakistan: Deh Amilano Israel <sup>3</sup>	52	8	42	ISM	sSM		62	Present paper; LAY and NADLER, MS.
<i>G. henleyi</i>	Morocco: Goulimine Egypt: Burg el Arab <sup>3</sup>	52	10—14	36—40	?	?		62—66	WAIRMAN and ZAHAVI 1955
<i>G. amoenus</i>	Egypt: Abu Rawash, Fayum, Wadi Natroun <sup>3</sup>	52	11—13	42 39—41	ISM ?	sA		62, 61	Present paper
<i>G. garamantis</i>	Algeria <sup>3</sup>	54	?	?	ISM	ISM	?	63, 65	WASSIF et al. 1969
<i>G. dasypurus</i>	Egypt: Cairo-Suez Road <sup>3</sup>	60	9—10	50—51	?	?		69, 70	WASSIF et al. 1969
	Sinai: St. Catherine's Monastery <sup>3</sup>	60	8	52	?	?		68	LAY and NADLER, MS.
	Sinai: Monastery <sup>3</sup>	60	6—8	52—54	?	?		66, 68	WAIRMAN and ZAHAVI 1955
<i>G. simoni</i>	Egypt: Burg el Arab, Western Desert <sup>3</sup>	60	8—10	50—52	?	?		63, 69	WASSIF et al. 1969
<i>G. campestris</i>	Morocco: Esoira, Taroudannt Morocco: 29 km SW Goulimine Egypt: Qara, Siwa Oasis <sup>3</sup>	56	10	44	mM	sA	68	Present paper	
		57/58	9/10	46/48	mM	?sA	68	Present paper	
	Algeria: Beni Abbès <sup>3</sup>	56	?	?	SM	SM	?	69, 71	WASSIF et al. 1969
									MATTHY 1953

Abbreviations as in Table 1

obtained identical karyotypes for a specimen from eastern Morocco. The karyotypic differences between these specimens and topotypical *G. pyramidum* are complex and outlined under results and in Figure 2. Several morphological features distinguish crania of these two populations: tympanic and mastoid components of the auditory bullae are distinctly less voluminous in *G. pyramidum*; the anterior end of the basioccipital contacts the medial walls of both tympanic bullae and is relatively narrower in the Algeria-Morocco sample; the posterior palatine foramina are shorter and more constricted in the Algeria-Morocco sample; the nasal-frontal bone contact is broad in *G. pyramidum* and narrow in the Algeria-Morocco sample. These combined differences suggest that the Algeria-Morocco sample is not conspecific with *G. pyramidum*. Resolution of this problem will require additional study. We are presently unable to determine what available scientific name, if any, should be used in reference to this population. Comparison of our specimens with the types and samples of *G. pyramidum tarabulli* Thomas, 1902, *G. hirtipes* Lataste, 1882 and *G. riggenbachi* Thomas, 1903 in the British Museum suggests that the Algeria-Morocco population is morphologically most like *G. p. tarabulli* and that *G. hirtipes* and *G. riggenbachi* should each be regarded as distinct species. ELLERMAN's (1940) concept of *G. pyramidum* as a polymorphic species occurring widely across North Africa is questionable and should be carefully re-evaluated.

*G. campestris* shows  $2N = 56$  in samples from Egypt, Algeria and Morocco (Table 1). Our observations on chromosome morphology differ considerably from those described by WASSIF et al. (1969) who did not publish a karyotype. It is possible that they have identified certain acrocentric chromosomes as metacentric elements as their karyotypes reveal was done in the case of *G. gerbillus*. MATTHEY's (1953) identification of both sex chromosomes as submetacentric is based on sectioned material. Our data suggest that the Y is an acrocentric element. Chromosomal polymorphism of a centric fusion/fission type was noted in specimens from 20–29 km SW Goulimine, Morocco. The Robertsonian rearrangement involves one or two pairs of submetacentric autosomes. One specimen has a  $2N = 56$  containing 10 submetacentric and 44 acrocentric autosomes, five animals show  $2N = 57$  with 11 submetacentrics and 46 acrocentric autosomes, two examples display  $2N = 58$  with 8 submetacentric and 48 autosomes. This is the second known case of polymorphism in *Gerbillus*.

Our data show that the karyotypes of *G. nanus* and *G. henleyi* differ only in the morphology of the Y chromosomes. The karyotype of *G. amoenus* is apparently very similar to that of *G. henleyi* (WASSIF et al. 1969) and the karyotypes of *G. dasyurus* and *G. simoni* are nearly identical. Thus, six naked-footed species studied cytologically are readily distinguished using skin and skeletal characters but these species show relatively little chromosomal divergence; the taxonomic status of the seventh species, *G. garamantis*, is unclear and may represent *G. nanus*, but this view espoused by PETTER (1961) is undocumented. Among the hairy-footed species *G. allenbyi* and *G. andersoni* are morphologically and karyotypically very similar. The only karyotypic difference detected by our techniques is an apparent dissimilarity of the X chromosomes (Fig. 1). Less morphological (skin and skeletal) and more chromosomal diversity is characteristic of the hairy-footed species. Perhaps the disjunct nature of many of the restricted sandy habitats occupied by closely related hairy-footed *Gerbillus* species promotes genetic variation, possibly due to founder effects, that is reflected more in the karyotypes than in skeletal and external phenotypes.

Karyotypes are useful in distinguishing species of *Gerbillus*, especially when employed in conjunction with skeletal and external characters. The karyotypic diversity of the hairy-footed species suggests that the widely employed taxonomy of ELLERMAN and MORRISON-SCOTT (1951) has underestimated the taxonomic diversity

of these rodents. In depth modern studies of the evolutionary biology of *Gerbillus* populations are required to interpret the observed cytogenetic differences and to elucidate the systematics of this genus. Future work would be enhanced by utilization of chromosomal banding techniques and attempts to establish interspecific chromosomal homologies. Such an approach could help to establish the pathways of chromosomal evolution and taxonomic relationships in *Gerbillus*.

### Summary

Pertinent previous chromosomal data concerning the genus *Gerbillus* are reviewed. Karyotypes of *G. allenbyi*, *G. perpallidus*, *G. nanus*, *G. henleyi*, *G. dasyurus*, *G. campestris* and *G. sp.* (= ? *tarabulli*) are published for the first time. The karyotypes of *G. gerbillus*, *G. nanus* and *G. aquilus* are shown to be uniform over wide areas within their ranges. A Robertsonian chromosomal polymorphism is described in specimens of *G. campestris* from Morocco. Evidence is presented which shows that the diploid numbers within the chromosomally polymorphic population described by ZAHAVI and WAHRMAN (1957) and WAHRMAN and GOUREVITZ (1972) differ significantly from that of topotypic *G. pyramidum*. The data suggest that the Israel population and the Algeria population of ZAHAVI and WAHRMAN (1957) and *G. pyramidum* should each be considered as distinct species, pending in-depth future studies. Cytological data from six of the approximately 30 naked-footed and 13 of an estimated 20 hairy-footed *Gerbillus* species do not support the recognition of subgenera or the division of these rodents into two genera.

### Zusammenfassung

#### *Chromosomen einiger Arten von Gerbillus (Mammalia: Rodentia)*

Die Studie gibt einen Überblick über bisher vorliegende Daten zur Chromosomenstruktur einzelner Arten der Gattung *Gerbillus*. Zusätzlich werden Karyotypen von *G. allenbyi*, *G. perpallidus*, *G. nanus*, *G. henleyi*, *G. dasyurus*, *G. campestris* und *G. tarabulli* erstmals hier veröffentlicht. *G. gerbillus*, *G. nanus* und *G. aquilus* erweisen sich über große Bereiche ihres Verbreitungsgebietes in den Karyotypen als gleichförmig. Robertsonscher Chromosomen-Polymorphismus wird bei Exemplaren von *G. campestris* aus Marokko beschrieben. Auch ZAHAVI und WAHRMAN (1957) und WAHRMAN und GOUREVITZ (1972) machen Angaben über chromosomen-polymorphe Populationen. Nunmehr wird festgestellt, daß sich die Diploidzahlen dieser Populationen ganz erheblich von denen der topotypischen Art *G. pyramidum* unterscheiden. Bis auf vertiefte künftige Studien sind den Daten zufolge wahrscheinlich die israelischen und die algerischen Populationen von ZAHAVI und WAHRMAN (1957) wie auch *G. pyramidum* als verschiedene Arten zu führen. Cytologische Angaben von 6 der ca. 30 nacktfüßigen und von 13 der ca. 20 haarfüßigen *Gerbillus*-Arten rechtfertigen weder die Anerkennung verschiedener Untergattungen noch die systematische Einteilung dieser Nagetiere in zwei Gattungen.

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## Über die Wehentätigkeit des Kaninchens

### Eine elektrophysiologische Studie der Uterusaktivität und eine Theorie über die Auslösung des Geburtsbeginns

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#### 1. Einleitung

Obwohl das Kaninchen schon seit dem Beginn der experimentellen Forschungsmethoden in der Biologie und Medizin eines der am häufigsten gebrauchten Versuchstiere ist und besonders in der geburtshilflichen Forschung sehr oft benutzt wird, sind in der Literatur nur spärliche Angaben über die normale Geburt vorhanden. Viele